

Biogeography of Southeast Asia (and Wallacea) scorpions, a review

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Abstract: Biogeographic patterns observed among modern scorpions are the consequence of different major events which can be integrated in the schematic scales proposed by M. Udvardy. The distribution of the principal modern groups (i.e. families and genera) is derived from elements (protofamilies and protogenera of Pulmonate-Neoscorpionina) which originated in Pangea. The main factor in the phylogenetic/palaeobiogeographic scale was probably not the latitudinal and longitudinal overland migration (dispersion) of the ancestors Neoscorpionina, which followed the predominantly southward shift of the warm tropical belt, but a rather more passive vicariant process in association with dispersal in Haffer's sense, in response to the progressive fragmentation of Pangea. This was followed by continental drift which led to the present configuration of the continents and climates. This suggestion seems to be in accordance with the very poor vagility observed in modern scorpions. On the millennial scale, Pleistocene and post-Pleistocene biogeography has been responsible for the regional level of the distribution pattern which, during its settlement, has led to the selection of some new specific lineages and to the extinction of others. On the secular scale, the ecological biogeography is a consequence of recent natural or anthropic events. This scale has been little used by scorpion biogeographers, mostly because of lack of data on scorpion life history strategies. In this chapter, examples from Southeast (and Wallacea) scorpions are proposed for and discussed in relation to the three biogeographic scales of Udvardy.

Key words: Scorpion, Southeast Asia, Wallacea, biogeography, Pangea, Laurasia, Gondwanaland, Pleistocene, ecology.

Introduction

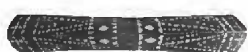
As already mentioned in previous publications (Lourenço 1996, 2003), some studies on scorpion biogeography are by no mean recent. Attempts began with the contributions of Pocock (1894a), Kraepelin (1905) and Birula (1917). Certain general patterns of distribution were then proposed, even though the viewpoints of the different authors were frequently not in agreement. These preliminary general contributions have been followed more recently by regional biogeographical studies such as those by Mello-Leitão (1945), Vachon (1952), Koch (1977), Francke (1978), Lamoral (1979) and Couzijn (1981). Nevertheless, most of these studies were enable to demonstrate precise biogeographical patterns. More recent studies, dealing mainly with Neotropical scorpions, make it possible to define some precise biogeographic patterns for these organisms (Lourenço 1986a,b, 1994, 1996a, 2002a,b, 2003). The definition of these has been possible thanks to

(i) a better knowledge of the phylogeny of several groups of scorpions (Lourenço, 2002a);

(ii) the application of recent hypothesis concerning climatic vicissitudes, especially in tropical biomes during the late Cenozoic and Pleistocene periods (Prance, 1982a);

(iii) a much better knowledge of scorpion life history strategies (Lourenço, 1991). According to Polis (1990) and Lourenço (1991) most, scorpions can be defined as being equilibrium species, presenting therefore very predictable patterns of distribution.

In two recent papers (Lourenço 1996a, b), a more detailed biogeographical model was proposed, based on Udvardy's (1981) division of biogeography into three spatio-temporal entities. This approach was adopted because it is both clear and didactic. Using it three major biogeographical events can be suggested to explain most of the patterns of distribution observed among scorpions today.



Scorpion biogeography patterns

1. Phylogenetic scale: palaeobiogeography

The phylogenetic scale encompasses the evolutionary time of all biota and is limited in space only by the size of the earth (Udvardy 1981). On this scale, only historical factors can be assumed to have taken place since, for almost all ecological conditions, data are largely or totally unknown. At this level, the evolutionary process of biogeography is, to a considerable extent, a tributary of continental drift and plate tectonics. This new view shook the foundations of the theories of many older paleontologists and biogeographers (Udvardy 1981).

Few authors (e.g. Lamoral 1979, 1980; Couzijn 1981; Nenelin & Fet 1992; Lourenço 1996a, b; Monod & Lourenço 2005) have taken continental drift into consideration when discussing aspects of regional biogeography. Lamoral's (1980) suprageneric classification of recent scorpions, with discussion on their zoogeography, was an important attempt to explain the general patterns of scorpion biogeography. The zoogeographical suggestions which Lamoral made are generally acceptable: (1) the present global scorpion fauna is derived from elements of the pulmonate (Neoscorpionina) that originated in Laurasia and Gondwanaland during Pangean times, (2) the protobuthids were the dominant fauna in Pangea, and the distribution of present Buthidae is the result of a vicariant process emanating from the fragmentation of Laurasia and Gondwanaland; (3) other early ancestors of scorpions such as the Chaeriloids, Chactoids, Pseudochactoids and Scorpionoids, also evolved in Laurasia and/or Gondwanaland in this past-period. The more detailed conclusions of Lamoral (1980) are mainly correlated with vicariance and with continental drift. Lamoral (1980) failed, however, to explain some important points. There is no doubt that he insisted too much on the role of dispersion when affirming that two major factors have influenced speciation and distribution patterns. One is the fragmentation of Pangea and Gondwanaland; the other is the movement of Laurasian elements to the North of Gondwanaland. This second factor should be reconsidered. The process of 'active' dispersion should rather be interpreted as being a more 'passive' process in Haffer's (1981) dispersal sense (To avoid making the subject too long, I do not discuss here the arguments of Platnick (1976), Udvardy (1981) and Haffer (1981) regarding their personal opinions about the meaning of

both dispersion and dispersal (see also Lourenço 1986b)). This argument can be supported by the poor vagility presented in modern species of scorpion (it might be suggested that primitive or aquatic scorpions were better able to disperse than terrestrial forms. They were therefore able to reach many of the shores of Pangea before and during the fragmentation process, since scorpions remained marine (or aquatic) from the Silurian until at least the Triassic (Briggs 1987; Shear & Kukalová-Peck 1990; Lourenço 1991)). Present biogeographic patterns may be considered more as the result of different vicariant processes, and as some pieces of an incomplete puzzle. Lamoral did not answer the question about the 'apparent anomalies in the distribution of some groups of families and genera'. These 'anomalies' have been discussed since the publication by Pocock (1894a). Even today the disjunctive distributions of several families and genera of scorpions remain unexplained. The cases of the present disjunctive distribution of some scorpion groups should be regarded as the result of the previous distribution of protoelements of families and genera, followed by a vicariant process. The exact mechanism of the process has not, however, yet been explained.

Consequently, it can be suggested that the main event responsible for the biogeographic patterns of distribution of scorpions, on a palaeogeographic scale, was the fragmentation of Pangea and subsequent continental drift. The difficulties in explaining the significant discontinuous distribution of some familial and generic groups point not only to the great geological age of these groups, but also to the relict faunas and biogeographical patterns which they exhibit today.

2. Millennial scale: Pleistocene biogeography

Between the development of the earth's crust and the Pleistocene epoch several events took place, many of which were related to the continuous drift of the continents. Without citing an exhaustive list, the following can be mentioned: mountain building, differential erosion, epicontinental seas, climatic-vegetational fluctuations, changes of world sea level and the formation of major river systems. All these events took place during the Cenozoic over a period of 60 My, and have influenced the present biogeographical patterns of scorpions. In this section special reference is made to one of these events, climatic-vegetational fluctuation, which played a major role since the late



Cenozoic and which has had a major impact during Pleistocene times (for a better understanding of the astronomical basis of the climatic oscillations - 'Milankovitch cycles' - see Haffer (1993)). For more details of the consequences of the other events, refer to Haffer (1981).

For many years, books and papers about the tropical regions have stated that the biogeographical and diversity patterns observed in these regions could be explained by the long stability of tropical forests over millions of years (Federov 1966; Richards 1969). Subsequent work on geology, paleoclimates and palynology, especially in Amazonia and Africa (Prance 1982a; Moreau 1963; Livingstone 1975, 1982), has demonstrated that this presumed stability was a fallacy (similar data for Asia and Southeast Asia is less available). In fact, although the temperatures in tropical lowlands remained 'tropical' during glacial periods (3-5°C lower than today), the forest broke into isolated remnants during cool dry periods (glacial phases). The remnants of forest expanded and coalesced during warm humid periods (interglacial phases). Conversely, nonforest vegetation expanded during glacial and retreated during interglacial phases (as at present). Data from geoscience, however, have been insufficient to indicate the precise areas of changing forests and nonforests and, in particular, the areas in which forests remained during arid phases, presumably serving as refugia for animal and plant populations. Nevertheless, in the Neotropical region, studies on the biogeographical patterns of scorpions (Lourenço 1986c, 1987) have indicated several endemic centres which are well correlated with the conclusions of Prance (1982b) on woody plants, and Haffer (1969) on birds.

3. Secular scale: ecological biogeography

The analysis of ecological factors responsible for explanation of the biogeographic patterns of scorpions have been biased on two major considerations:

(i) for many years there has been an almost total lack of knowledge of life history strategies; knowledge which, until the late 1980s, was almost the only preoccupation of ecologists,

(ii) a generalized opinion, even among modern biologists, according to which scorpions are capable of withstanding radical changes in environmental conditions, and therefore of being very good colonisers.

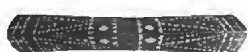
This assumption is a fallacy. With our growing

knowledge of scorpion life history strategies we can see that many, if not most scorpions, are equilibrium species (Polis 1990), which tend to inhabit stable and predictable natural environments, produce single egg clutches, do not store sperm, have long life-spans, present low population densities, have a very low r_{max} , show weak mobility, and are highly endemic.

In contrast, however, some scorpions are 'opportunistic species'. These include certain species of the family Buthidae and a few of the families Euscorpiidae and Liochelidae. They are marked by ecological plasticity and are readily capable of invading disturbed environments. They may produce multiple clutches from a single insemination, have elaborate sperm storage capabilities (Kovoor et al. 1987), short embryonic development, short life spans, high population densities, rapid mobility, and are widely distributed. The study of these opportunistic species is of little use for establishing biogeographical patterns.

Opportunistic species evolve mainly in disturbed and unpredictable environments which are the result of natural causes such as volcanic activity or human action. Examples include a population of the neotropical species *Centruroides gracilis* (Latreille, 1804) in the Canary Islands (Kraepelin 1905; Lourenço 1991) and the worldwide distribution of the originally Sri-Lankan species *Isometrus maculatus* (DeGeer, 1778) which has been transported by human agency during the last four centuries and is today present in almost all tropical coastal regions (Huber et al. 2002). The replacement of species is well illustrated in several islands of Eastern Asia (and Wallacea) where natural volcanic activity and human impact are important (Vachon & Abe 1988). In this region, many endemic populations of equilibrium species are regressing or have disappeared. Some may be replaced by opportunistic species which will probably occupy most of the islands in the future (Vachon & Lourenço 1985).

In continental regions, opportunistic species can rapidly occupy habitats disturbed by human activities, where the original native species have been selected against, thus leaving their ecological niches vacant (Lourenço & Cloudsley-Thompson 1996). This kind of situation is yet rarely observed in Southeast Asia (and Wallacea), except maybe, for the expanding distribution of species such as *Isometrus maculatus* (DeGeer, 1778), *Lychas mucronatus* (Fabricius, 1798) and *Liocheles australasiae* (Fabricius, 1775).



Biogeographical patterns in Southeast Asia (and Wallacea)

Since it is not in the scope of this chapter to provide an exhaustive description of the geology of Southeast Asia (and Wallacea), only a synopsis is proposed of the excellent contributions by Moss & Wilson (1998), Turner et al. (2001) and Michaux (2010), including several references therein.

As stated by Turner et al. (2001), the biogeography of Southeast Asia and the West Pacific is complicated by the fact that these are regions on the border of two palaeocontinents that have been separated for a considerable period of time. Thus, two general patterns relating to dispersal can be found: a group of Southeast Asian elements, perhaps of Laurasian origin, expanding into Australian areas, and a reverse pattern for Australian elements, perhaps of Gondwanan origin. Besides, both Australian and Southeast Asian elements may occur in the Pacific. They dispersed there as the Pacific plate moved westward, bringing the different islands within reach of Southeast Asia and Australia.

The Malay Archipelago, also known as Malesia (Malaysia up to the Philippines and Papua New Guinea), also has a very complex geological history. Several larger islands are complexes of amalgamated microplates and almost all microplates originated from the Australian plate or Australian part of Gondwana. The western half of Malesia (up to Borneo and a part of Sulawesi) broke off first and was already well in place before the second wave of microplates started to move away from Australia. In the case of modern taxa of several groups the western half of Malesia is an extension of Southeast Asia. Taxa that are widespread and cross Wallace's line in the centre of Malesia, could only have obtained their distribution after dispersal for which, theoretically, various routes have been available. Several parts of the microplates emerged above water and could be used as 'stepping stones' during dispersal.

The collisions between several ocean plates (Pacific, Indian, Philippine) and land plates (Eurasian, Indian, Australian) have created an intricate geological history for Southeast Asia and the West Pacific islands (see Ridder-Numan 1996) and for the East Malay Archipelago and the West Pacific Islands (de Boer 1995; de Boer & Duffels 1996).

The West Malay Archipelago and part of Southeast Asia consists of fragments which broke off from Australia and which rifted northwards and

collided with the Eurasian Plate. This process may already have started in the early Palaeozoic (circa 400 My) or up to the Late Devonian. Consequently, most of Southeast Asia was already in place before many recent plant and animal taxa evolved there. Thus the plants and animals present in West Malesia should be mainly of Southeast Asian origin. The history of the plants and animals may still reflect part of the geological history of this region as many microplates remained separate for a long time, or after collision had created barriers like mountain ranges. Moreover, large parts of Southeast Asia and West Malesia were submerged several times, not only during the more recent interglacial periods, but high sea levels were for instance also present during the Late Eocene (circa 40 My). India separated from Gondwanaland circa 195 My, and finally collided with Asia in the Late Eocene. India could have acted as a 'raft', carrying taxa from Africa to Asia, which could spread over Southeast Asia and West Malesia after collision. During its rift it came in close contact with still northward moving Sumatra, which means that an earlier exchange of floral and faunal elements could have taken place. Possibly, during the close contact between Sumatra and India, India became populated by Southeast Asian elements, still existing in the forests of Kerala and Sri Lanka. The East Malay Archipelago also consists of small fragments of Australian-New Guinean origin. These include East Sulawesi, the Moluccas and the Lesser Sunda Islands. With the arrival of these slivers and after their emergence from sea, several island arcs were formed between Southeast Asia and Australia. As stated by Turner et al. (2001), New Guinea has a very special history. 'The southern part (south of the central mountain ranges) has always been attached to Australia. The northern edge is an amalgamation of more than 30 terranes of various origins: island arcs, pieces of broken off Australian or New Guinean continent and even parts of trapped sea floor' (Turner et al. 2001).

As outlined by Turner et al. (2001), 'the regions of Southeast Asia and the West Pacific have long attracted the attention of biogeographers. In the 19th century Alfred Russel Wallace noted that the biota of the Malay archipelago consisted of Asian and Australian elements, with the former predominant in the western part, and the latter towards the east. His explanation was that the different groups of organisms had originated in Asia and Australia, and subsequently dispersed. Also, he assumed that these continents had at one time been larger, and became fragmented as a result of



sea level fluctuations. Wallace (1860) drew a line demarcating where the Asian biota is separated from the Australian one, later called 'Wallace's Line'. Mayr (1944) used the name Wallacea for the region between Wallace's and Lydekker's lines. According to Michaux (2010), however, Wallacea as a whole cannot be considered as a natural biogeographical region, neither is it completely artificial as it is formed from a complex of predominantly Australian exotic fragments linked by geological processes within a complex collision zone.

According to some authors, Moss & Wilson (1998), Wallacea includes Sulawesi, the Moluccas and the Lesser Sunda Islands as well as an extensive area of shallow sea, and its eastern margin is taken as Lydekker's line; the western boundary of the strictly Australian fauna. Other authors (see Michaux 2010) argued that the Philippines may be an integral part of Wallacea.

The scorpions of Southeast Asia (and Wallacea)

As already outlined in several publications (Lourenço 2007, 2009a, 2011a, b, c, 2012a, b; Lourenço & Duhem 2010a, b; Lourenço & Leguin 2012; Lourenço & Pham 2011, 2012; Lourenço & Zhu 2008; Lourenço et al. 2010a, b), the scorpion fauna of Southeast Asia (and Wallacea) has been poorly studied. Pioneer work has been conducted by many authors, but most of their publications represent isolated contributions, e.g. Gervais (1841, 1844), Oates (1888), Pocock (1891, 1894b), Simon (1877, 1878, 1893), Thorell (1888, 1889, 1890), Borelli (1904), Banks (1928), Fage (1933, 1936, 1946), Kopstein (1935, 1937) in which new taxa were described. Subsequently, a number of new contributions have revealed additional new species or interesting aspects about the elements of this fauna, such as the papers by Takashima (1942, 1945, 1948, 1950, 1952), Bristowe (1952), Francke (1976), Koch (1977), Couzijn (1981), Vachon & Lourenço (1985). More recently, other contributions have appeared Kovařík (2000, 2003, 2012) but are generally poorly documented and illustrated. Some, however, are much better documented and especially well illustrated than others, conveying a better understanding of the scorpions of Southeast Asia (e. g. Lourenço 2007, 2009a, b, 2011a, b, c, 2012a, b; Lourenço & Duhem 2010a, b; Lourenço & Leguin 2012; Lourenço & Pham 2010, 2012; Lourenço & Zhu 2008). Very recent studies have led to the description of new species of *Chaerilus* Simon, *Isometrus* Ehrenberg,

Lychas C.L. Koch and naturally of pseudochactids from Cambodia, Laos, Vietnam but also from Indonesia and Papua New Guinea (Lourenço 2007, 2009a, b, 2011a, b, c, 2012a, b; Lourenço & Duhem 2010a, b; Lourenço & Leguin 2012; Lourenço & Pham 2010, 2012; Lourenço & Qi 2007; Lourenço & Zhu 2008; Lourenço & Ythier 2008; Lourenço et al. 2010, 2011).

Naturally, the most remarkable discoveries and descriptions of recent years were those of the elements of the enigmatic family Pseudochactidae Gromov, 1998, previously known only from Tajikistan and Uzbekistan (Lourenço 2007). Two new genera *Troglokhammouanus* Lourenço, 2007 and *Vietbocap* Lourenço & Pham, 2010 and four new species, *Troglokhammouanus steineri* Lourenço, 2007, *Vietbocap canhi* Lourenço, Pham, 2010, *V. thienduongensis* Lourenço, Pham, 2012 and *V. lao* Lourenço, 2012 from caves in Laos and Vietnam (Lourenço 2007, 2012; Lourenço & Pham 2010, 2012). The biogeographical impact of these discoveries in Southeast Asia will be the subject of future contributions (Lourenço, in preparation).

In this chapter, I propose only a synopsis of the major scorpion groups present in Southeast Asia (and Wallacea). Any resolution to the species level is not possible at this stage since many species remain dubious and require further investigation.

Family **Buthidae** C.L. Koch, 1837

Genus ***Isometrus* Ehrenberg, 1828** (Fig. 1, map 1)

The genus *Isometrus* with its two subgenera *Isometrus* Ehrenberg and *Reddyanus* Vachon is a typical Asian and Oceanic element with a rather widespread distribution in these regions. Within Southeast Asia and Wallacea it is distributed in Cambodia, Indonesia (Java, Sumatra, Borneo), Laos, Malaysia, Myanmar, New Guinea, Philippines, Singapore, Thailand and Vietnam. Outside this area it is also present in Australia, China, India, New Caledonia, Solomon Islands and Sri Lanka. One species, *Isometrus* (*Isometrus*) *maculatus* is the most widely distributed scorpion species in the world, and can be found in most tropical and subtropical coastal regions. Its distribution, however, has an anthropogenical background, probably going back to the great naval voyages of the 16th century. So it can only be considered as a secondary succession of an opportunistic element (Huber et al. 2002).

Elements found in Tertiary Baltic amber (circa 55 My) suggested closely connections between this palaeofauna and elements of the genus *Isometrus*. This can suggest that this genus presented in





Figure 1. *Isometrus lao* Lourenço, Leguin, 2012. Male holotype from Laos.

palaeotimes a much wider distribution than the present one (Lourenço & Weitschat 2005; Lourenço 2009c).

Genus ***Lychas* C.L. Koch, 1845** (Fig. 2, map 1)

The genus *Lychas*, which clearly presents phylogenetic connexions with the genus *Isometrus*, shows a much larger distribution over Africa, Asia and Oceania. Within Southeast Asia (and Wallacea)

it is distributed in Cambodia, Indonesia Islands, Laos, Malaysia, Myanmar, New Guinea, Philippines, Thailand and Vietnam. Outside this area it is also present in several countries in Africa: Angola, Congo, Democratic Republic of Congo, Ethiopia, Kenya, Malawi, Mozambique, Somalia, South Africa, Tanzania, Zambia, and Zimbabwe. In the Indian Ocean Islands it is present in Mauritius and Seychelles, but curiously absent from Madagascar.





Figure 2. *Lychas aberlenci* Lourenço, 2013. Male from Laos (photo: A. Teynié).

Its distribution in Asia and Oceania comprises Andaman Islands, China, India, Japan (introduced), Nepal, Sri Lanka, Australia, Fiji, Solomon Islands.

The genus *Lychas* C.L. Koch, clearly presents a Gondwanian pattern of distribution which was globally suggested for the elements of the 'Ananteris-group' (Lourenço 2011d). This 'Group' includes also other genera such as *Ananteris* Thorell, 1891 in Tropical America, *Ananteroides* Borelli, 1911 and *Lychasioides* Vachon, 1974 in Africa, *Tityobuthus* Pocock, 1893 in Madagascar and *Himalayotityobuthus* Lourenço, 1997 in the Himalayas.

Other elements found in Tertiary Baltic amber (circa 55 My) equally suggested closely connections between this palaeofauna and elements of the genus *Lychas*. This can suggest that this genus presented in palaeotimes an even more wider distribution than the present one (Lourenço & Weitschat 1996; Lourenço 2009c, 2012d).

At least one species *Lychas mucronatus* (Fabricius, 1798) is very largely distributed in Asian

tropical forests. Its distribution, however, seems to be limited to Asia, not reaching New Guinea or Australia. Records for Japan are associated to an anthropic introduction. This species shows characteristics of a polymorphic species, as already observed for other buthid elements. However, most of its range of distribution can be attributed to a natural process of dispersion. Although this species is common in rainforests, its process of distribution and differentiation is still poorly understood and will require further investigation.

A third buthid genus *Thaicharmus* Kovarik, 1995 was also recently described from Southeast Asia, Thailand. It remains, however, rare and imprecisely known.

Family **Chaerilidae** Pocock, 1893

Genus ***Chaerilus* Simon, 1877** (Fig. 3, map 2)

Chaerilids are at present a typical Asian group of scorpions with a large number of species in Southeast Asia (and Wallacea). As Lamoral (1980) already suggested the protoelements of

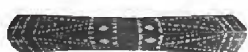




Figure 3. *Chaerilus telnovi* Lourenço, 2009. Male holotype from Halmahera.

the Chaeriloids most certainly evolved in Laurasia during Pangean times and only subsequently to the connection of India with the Asian continent their elements dispersed toward the south, to India, Southeast Asia (and Wallacea).

Species are known from Cambodia, the Indonesian Islands: Borneo, Celebes (Sulawesi), Java, Sumatra (and more recently from Halmahera), Laos, Malaysia, Myanmar, Philippines, Singapore,

Thailand and Vietnam. This family is also known from the Andaman Islands, Bangladesh, China, India, Nepal and Sri Lanka (Lourenço 2001a, 2012b).

A few and rare elements found in Cretaceous Burmese amber (circa 110-120 My) clearly suggested closely connections between the Cretaceous palaeofauna and extant species of the family Chaerilidae (Santiago-Blay et al. 2004).





Figure 4. *Euscorpiops alexandreaanorum* Lourenço, 2013. Male holotype from Laos (photo: A. Teynié).

This suggests that elements associated to the chaerilids were already presented in palaeotimes of continental Southeast Asia.

Family **Euscorpiidae Laurie, 1896** (Fig. 4, map 3)
Subfamily **Scorpiopinae Kraepelin, 1905**

The family Euscorpiidae has a very wide distribution from Southeast Asia through Middle East, Europe and North America (Lourenço 2013). This pattern of distribution clearly attests of a Laurasian origin. In Asia and Southeast Asia only the elements of the subfamily Scorpiopinae are represented by six genera: *Alloscorpiops* Vachon, 1980, *Dasyscorpiops* Vachon, 1974, *Euscorpiops* Vachon, 1980, *Neoscorpiops* Vachon, 1980,

Scorpiops Peters, 1861 and *Parascorpiops* Banks, 1928. All excepted one, *Neoscorpiops* known only from India, are represented in Southeast Asia, but most are only distributed in the continent: Laos, Myanmar, Thailand and Vietnam. The only element present in Wallacea is *Parascorpiops* Banks represented by a single species from Borneo/Sarawak. This subfamily is also distributed in Afghanistan, Bangladesh, Bhutan, China, India, Malaysia, Nepal and Pakistan. No fossil records are known (Lourenço 2013).

Family **Liochelidae Fet, Bechly, 2001**

Genus ***Liocheles* Sundevall, 1833** (Fig. 5, map 1)

The family Liochelidae presents a typical





Figure 5. *Liocheles australasiae* (Fabricius, 1775). Female from Vietnam (photo: E. Ythier).

Gondwanian pattern of distribution. In Southeast Asia (and Wallacea) it is represented by one genus *Liocheles* Sundevall. It can be suggested that the elements of the liochelids were already present in the emerged shields of Gondwanaland prior to the continental fragmentation that took place in the second half of the Cretaceous (Lourenço 1989).

In Southeast Asia and Wallacea *Liocheles* Sundevall species are distributed in Cambodia, Laos, Indonesian Islands, Malaysia, Myanmar, Papua New-Guinea, Philippines, Thailand and Vietnam. Besides this region, the group is also distributed in Bangladesh, China (this record needs further confirmation), India, Japan (south islands), Australia, South Pacific islands, New Caledonia, Solomon Islands and Vanuatu. Another genus, described from south of Vietnam, *Hormiops* Fage, 1933, remains dubious.

Only one fossil element associated to the Liochelidae family was described from the Early Cretaceous of Brazil, representing in fact a proto-element to the liochelids. This sedimentary fossil brought some further evidence to the Gondwanian pattern of distribution observed for this family. The discovery of *Protoischnurus axelrodorum* Carvalho,

Lourenço, 2001 (Protoischnuridae), in the Araripe Basin, within the Mesozoic interior basin of Brazil, suggests the association of extant ischnurids (liochelids) with lineages at least 110-115 My-old. This finding corroborates the conclusion according to what liochelids lineages must have existed in the Cretaceous previous to the Gondwana break-up (Carvalho & Lourenço 2001).

Family **Pseudochactidae Gromov, 1998** (Fig. 6, map 4)

Genus ***Troglokhamouanus* Lourenço, 2007**

Genus ***Vietbocap* Lourenço, Pham, 2010**

Studies of the first species described for this family, *Pseudochactas ovchinnikovi* Gromov, 1998, insisted about the restricted distribution of this monotypic family to the mountains of Uzbekistan and Tajikistan (Lourenço 2007). It was also suggested that based on its ancestral position in scorpion phylogeny, the Pseudochactidae lineage probably evolved during the Permian/Triassic. It was also assumed, however, that it was impossible to speculate as to whether this lineage was localized or widespread since there are no fossils available and the family was represented by a





Figure 6. *Vietbocap thienduongensis* Lourenço, Pham, 2012. Male from Vietnam (photo: D.-S. Pham).

single monotypic genus. The Pseudochactidae, the most primitive extant group of scorpions, according to several authors, appears to have survived in such relict conditions (see Lourenço 2007).

The discoveries of two new genera and species of Pseudochactidae in a Laotian and Vietnamese cave systems re-opened the question about the palaeo-biogeographic origin of this lineage (Lourenço 2007, 2012; Lourenço & Pham 2010, 2012). The only possible land connection between Uzbekistan/Tajikistan and Laos/Vietnam is the old Asian core. Consequently, the present known geographic disjunction in members of this family reflects a much larger past geographic area of the lineage, and the hypothesis of a possible

Pangaeian origin (Permian to Triassic time), should to be reconsidered. A new species of the genus *Pseudochactas* Gromov, 1998 was recently described from Afghanistan (Soleglad et al. 2012).

Some recent, but very rare species found in Cretaceous Burmese amber (circa 110-120 My) possibly suggested that some elements of the Cretaceous palaeofauna could have some common relationships to the extant families Buthidae, Chaerilidae and Pseudochactidae (Lourenço & Beigel 2011; Lourenço, 2012c). This suggests that possible proto-elements associated to these three extant families may already have been present in palaeotimes of the continental Southeast Asia.

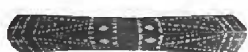




Figure 7. *Heterometrus laoticus* Couzijn, 1980. Female from Laos (photo: E. Ythier).

Family **Scorpionidae Latreille, 1802**

Genus ***Heterometrus* Ehrenberg, 1828** (Fig. 7, map 5)

Scorpions of the family Scorpionidae, are represented by species of large size, rather common in Southeast Asia (and Wallacea). These scorpions represent also the most recently evolved scorpions in this region. Species are distributed in Cambodia, China (south), Indonesian Islands, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand and Vietnam. The group is also present in Brunei, China (Tibet), India, Nepal and Sri Lanka.

No fossil records are known for this group of scorpions.

Possible Origins and affinities of the Southeast Asia (and Wallacea) scorpion fauna

Attempts to explain the origins and affinities of the scorpion fauna of Southeast Asia and in particular of Indonesian Islands and Wallacea, are not recent. Vachon (1953) during a symposium organized by the Biogeography Society in Paris

proposed already a number of theories to explain the distribution of the scorpions in this region, in particular in connexion to Wallace's line. More recently Couzijn (1981) also suggested a number of theories to explain the present, and possible past distribution of the genus *Heterometrus* Ehrenberg. Naturally, many if not most of these preliminary theories could be biased by a lack of a precise taxonomic knowledge of the groups distributed in the region.

In view of the tables already present in the previous sections, it seems reasonable to suggest that the patterns of distributions of some scorpion groups present in Southeast Asia (and Wallacea), may have a direct connection with panbiogeography models. These suggestions can be applied to the buthid genera *Lychas* C.L. Koch and in part *Isometrus* Ehrenberg, the liochelid genus *Liocheles* Sundevall, most of the Asian genera of Euscorpiid and to all chaerilid and pseudochactid elements. The situations of the the genus *Heterometrus* Ehrenberg is less evident, mainly by a total absence of known fossils.

Obviously the panbiogeography patterns are



directly related to the progressive fragmentation and continental drift of Pangea and Gondwanaland, but this model is responsible only of the original emplacement of proto-elements of the groups observed today. Subsequently, other events took also place, in particular connected with active or passive dispersal processes. For instance, the process of colonization of the different Indonesian islands by several scorpion elements are most certainly associated with the events that reduced the isolation of the islands as a consequence of the lowered sea levels during the extensive glaciations of the Pleistocene or previous periods. Sea levels were lowered 100 to 150 m (Donn et al. 1962; Gascoyne et al. 1979; Cronin et al. 1981; Mani 1974) exposing a series of 'stepping stone' islands from continental Southeast Asia up the nearby islands but also from island to island. The distance between the continent and the islands, and in particular between the islands was reduced in an important way.

Very recent natural or anthropogenic events are also responsible for some observed patterns of distribution. This includes important volcanic activities such the event of the Krakatau which took place in the end of the 19th century. Today a new scorpion fauna can be observed as the result of secondary succession (Vachon & Abe 1988). As already explained in the previous sections, the dispersion of some species by anthropogenic vehicles must to be retained. Species such as *Isometrus maculatus* (DeGeer, 1778), *Lychas mucronatus* (Fabricius, 1798) and *Liocheles australasiae* (Fabricius, 1775), most certainly have been transported by human agency during the last centuries, and still are today. Consequently these species are distributed in many tropical coastal regions of Asia, Oceania and Indian islands, as attested by the recently discovery of *L. australasiae* in the island of Reunion (Lourenço, unpublished data). In this volcanic island, native scorpion species are originally absent (Lourenço, unpublished data).

Conclusions

Although a reduced number of opportunistic scorpion species may not be good indicators for predictable biogeographic patterns, many or most scorpions are equilibrium species and can be useful models in biogeographical research. Several factors make scorpions useful for biogeographical (or biodiversity) studies, as suggested by Noss (1990):

- (i) stabilized taxonomy, at least for some regions of the world;
- (ii) life history strategies that are well understood;
- (iii) the fact that individuals can readily be observed in the field with the use of UV light, and
- (iv) biogeographical and endemic patterns that are well correlated with those of other taxa of animals and plants (see Lourenço 1987).

Scorpion biogeographers, however, need to be more aware, in their interpretations, of the distinction between the historical and the ecological factors responsible for the biogeographical patterns observed.

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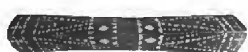
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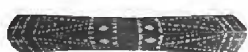
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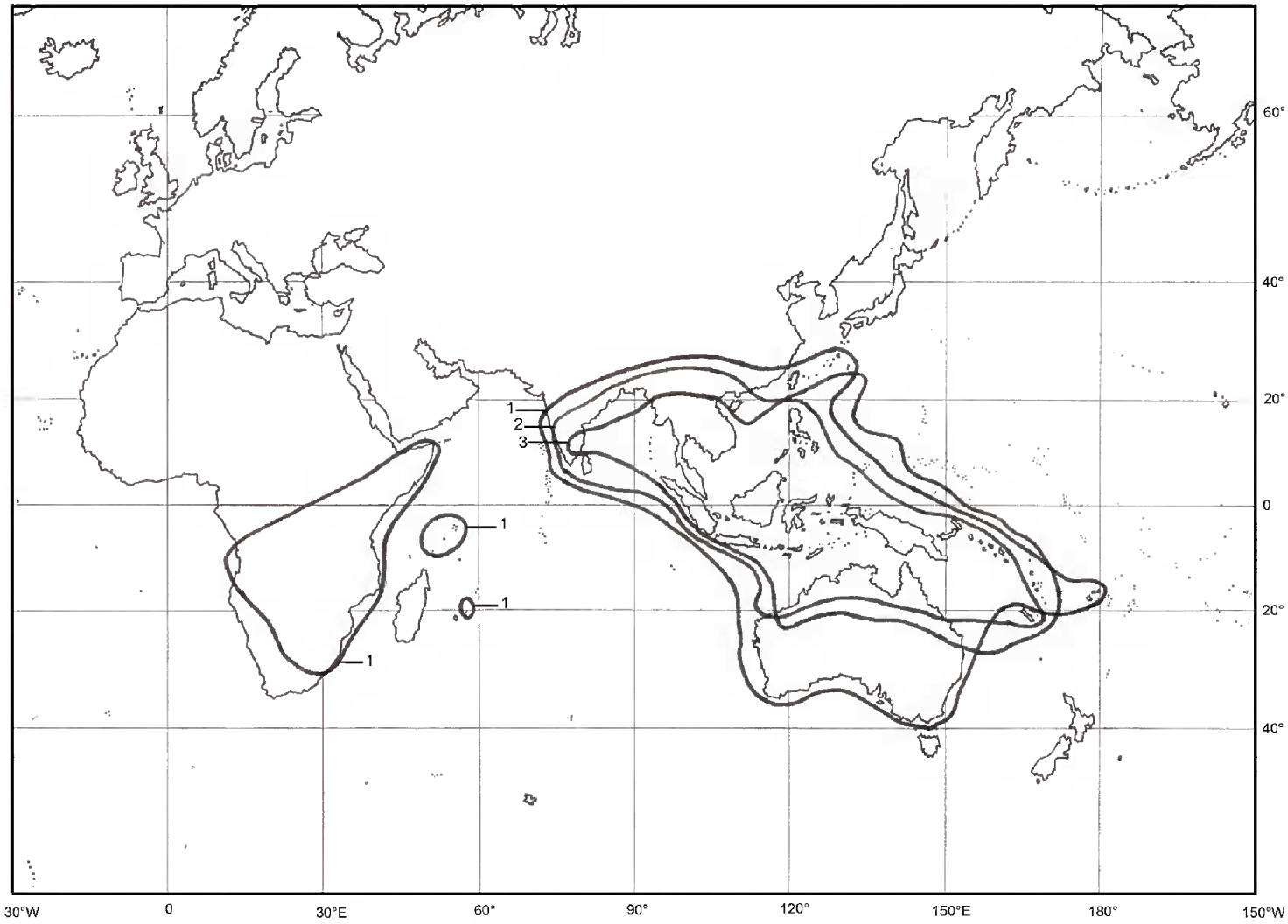


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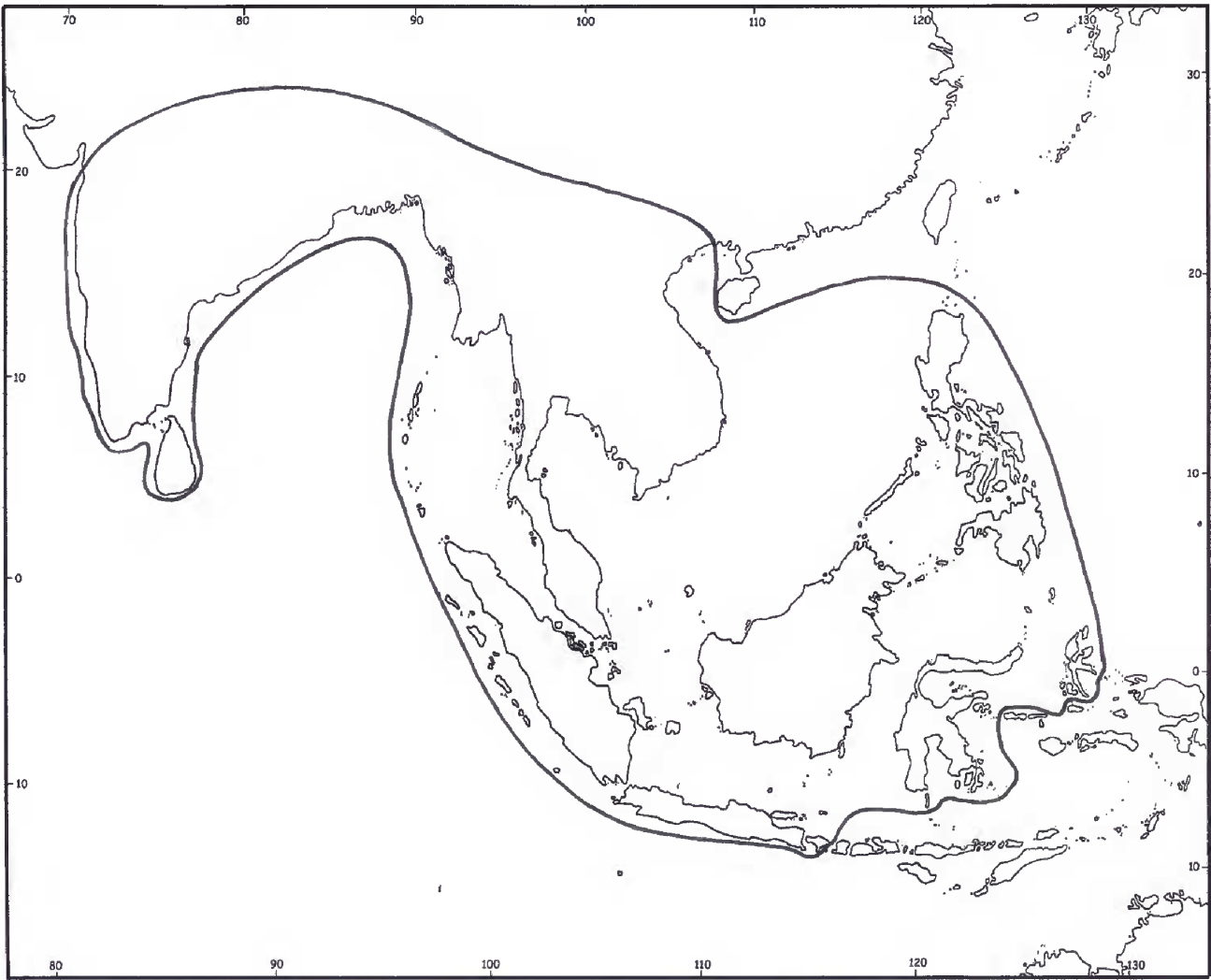


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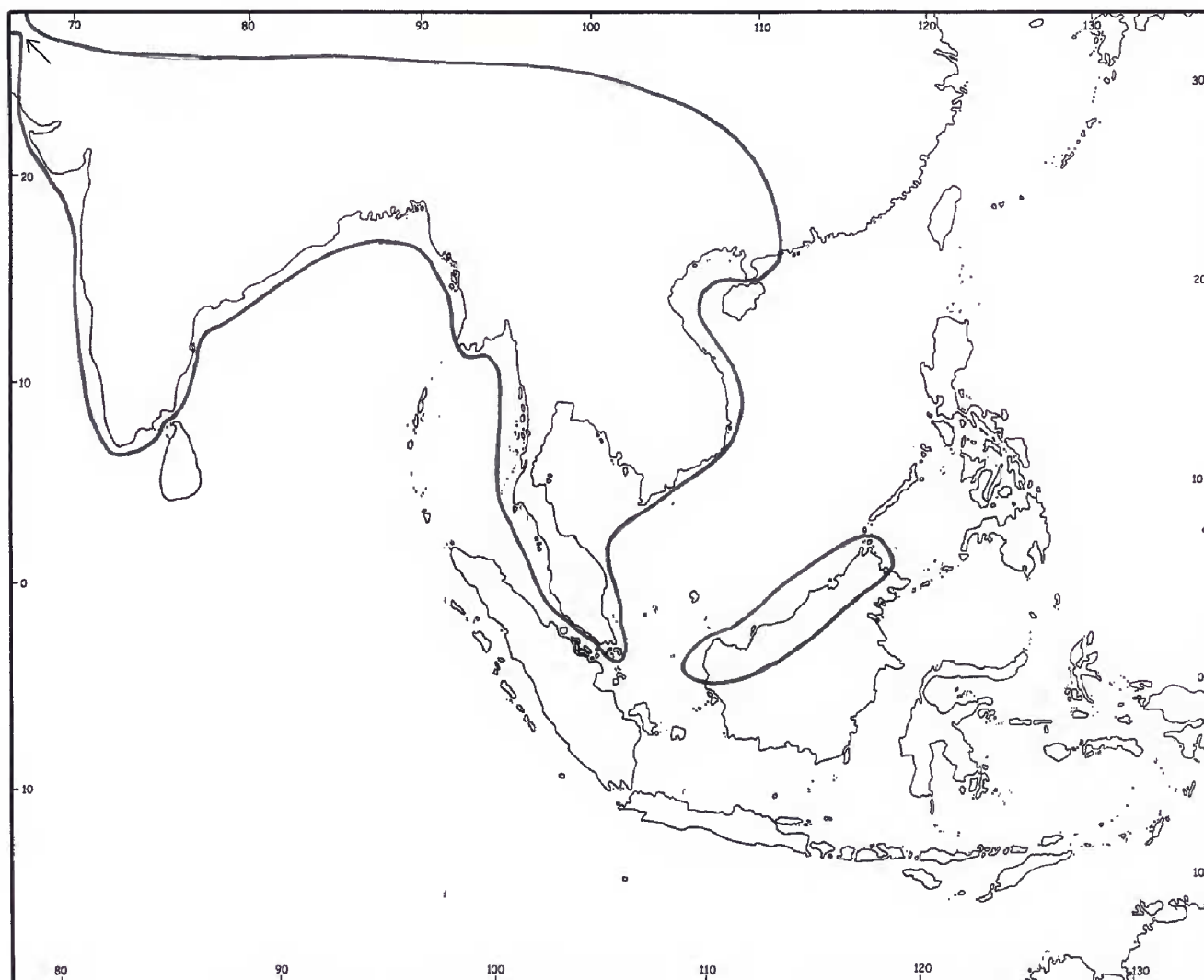


Map 1. Distribution area of genera *Lychas* C.L. Koch, 1845 (1), *Isometrus* Ehrenberg, 1828 (2) and *Liocheles* Sundevall, 1833 (3).

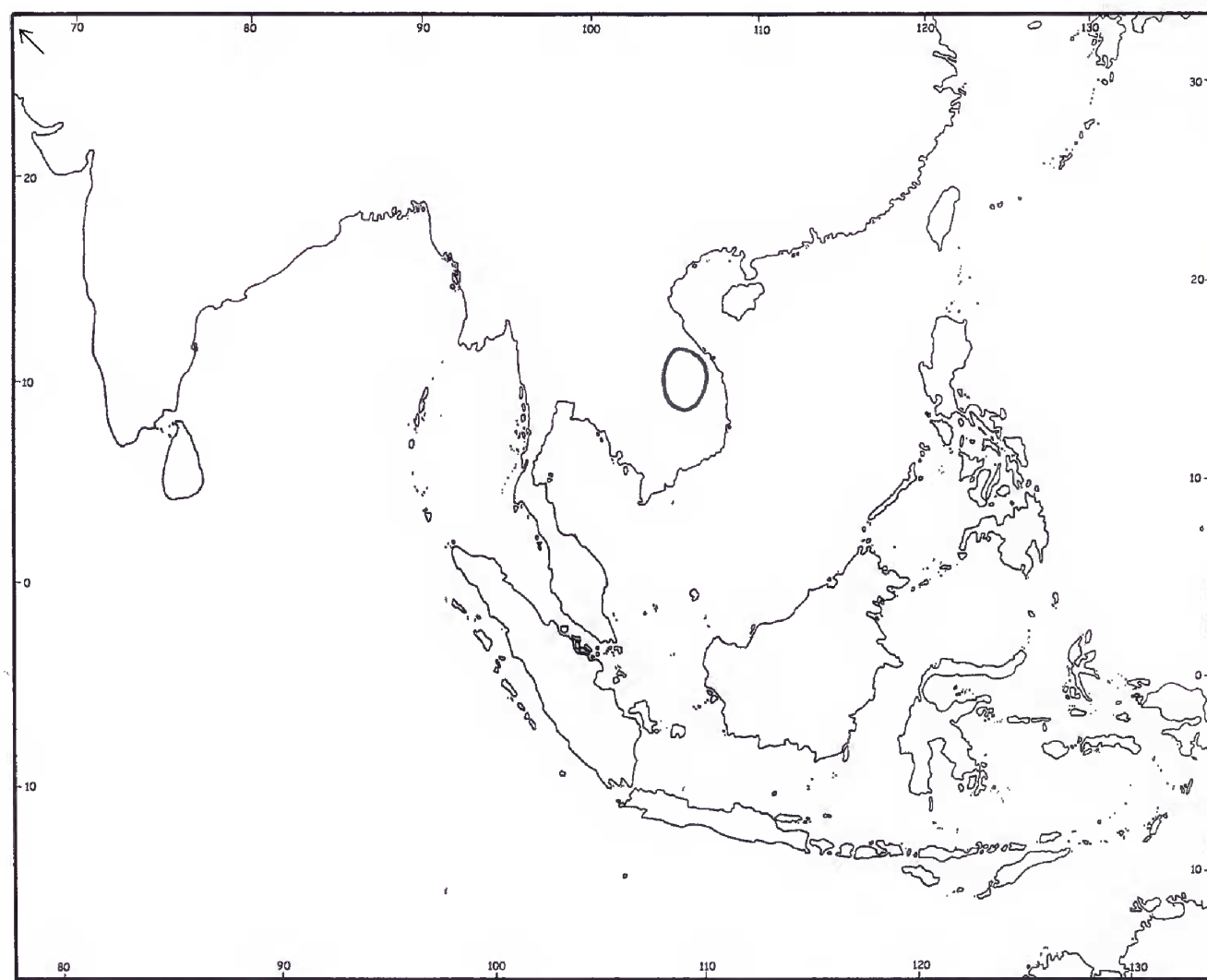


Map 2. Distribution area of the genus *Chaerilus* Simon, 1877.



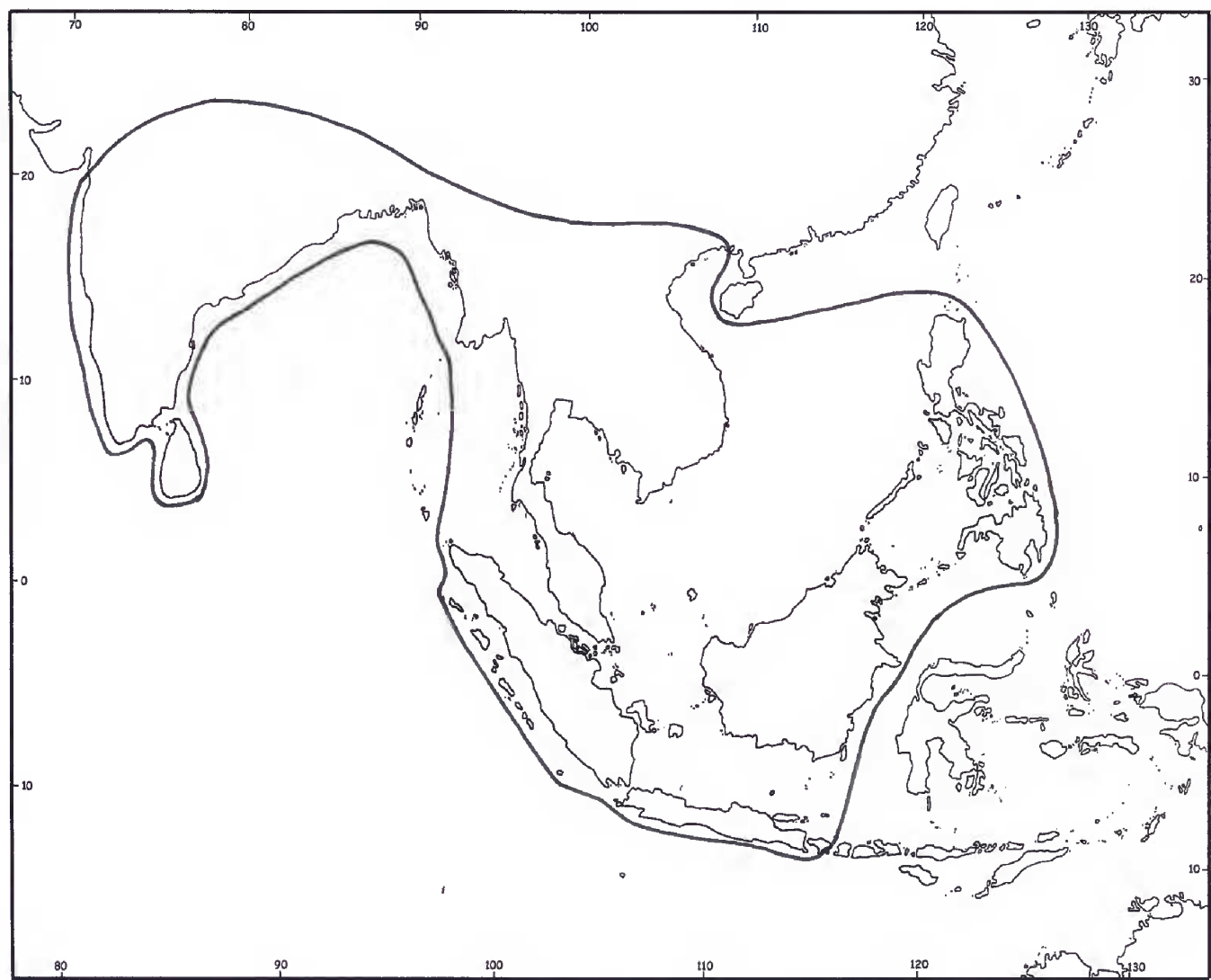


Map 3. Distribution area of subfamily Scorpiopinae. Arrow indicates that the family is also distributed westwards.



Map 4. Distribution area of family Pseudochactidae in Southeast Asia. Arrow indicates that the family is also distributed westwards.





Map 5. Distribution area of genus *Heterometrus* Ehrenberg, 1828.

